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THE NATICOID GENUS STROPHOSTYLUS.[1]

BY CHARLES R. KEYES.

AMONG the well-marked generic groups defined by Conrad is one to which the name Platyostoma was applied. This term was proposed in 1842;[2] and since that time it has come into common use in American Paleontology. The group embraces a considerable number of familiar species, ranging in geologic time from the Niagara epoch to the close of the Paleozoic. It is rather unfortunate, therefore, that the term had been preoccupied, having been used in generic diagnoses on at least four different occasions. Megerle early applied this name to certain mollusks closely related to Buccinum; but so far as is known no formal publication of the term was ever made. Were this the only obstacle in the way, Conrad's genus might be allowed to stand, for the reason that Megerle's proposition was only in manuscript. Klein,[3] however, proposed *Platystoma* in 1753 for a genus of Cyclostomacea. Meigen[4] adopted the same term in 1803 for certain flies, and Agassiz,[5] in 1829, also used it for a section of Silurid fishes. The preoccupation of Conrad's Platyostoma by Klein's Platystoma, like a number of similar cases, has been objected to on the ground that the two terms, while derived from the same words, are not identical, because Conrad's compound has a connecting *o*. It is quite manifest, however, that both generic words are taken from *platys* and *stoma;* and that from these it was the intention of Conrad to construct a correct generic term. In this attempt he used by mistake the connecting *o*, which is necessary in forming compounds from most Greek words, but which in the present instance was not called for, since the term is formed directly without the intervention of a copulatory vowel. For these reasons Conrad's and Klein's proposals cannot be regarded as distinct.

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[1] Read before the Iowa Academy of Sciences, September 5, 1890.

[2] *Jour. Acad. Nat. Sci.*, Phila., Vol. VIII., p. 275.

[3] Teut. Meth. Ostr., 1753.

[4] *Illig. Mag.*, Vol. II., 1803.

[5] *Pois. Foss.*, Vol. II., 1829.

Since it is clear, then, that Platystoma cannot be retained for the American group of Paleozoic gastropods, some other term must be adopted. Fisher[6] has taken advantage of the questionable validity of Conrad's name, and has recently proposed Diaphorostoma for the same group, with *Platystoma niagarensis* Hall for his type. This writer places Hall's Strophostylus as a subgenus under Diaphorostoma; while Zittel[7] assigns Hall's section to a similar taxonomic rank, but under Platystoma. Had Conrad's type of Platyostoma not been a form midway between the two extremes of a series forming the group Fisher's name might be retained, but the type of Strophostylus is congeneric with *P. ventricosum;* and as this name is the next proposed it must be taken into consideration. Were it not for this fact two sections of this group of shells could be with great propriety made. As regards the term Strophostylus, it was established by Hall[8] in 1859 for certain shells closely related to Platystoma, but differing chiefly in having a slightly "twisted or spirally grooved columella."

Recently a large series of the most important species of both Platystoma and Strophostylus was examined and the matrix carefully removed from the apertural portions of many of the shells. The structural features disclosed in the various forms show a relationship between the two established genera that was long suspected. It is well known that the type of Conrad's genus —*Platystoma ventricosum* Con.—is a somewhat globose shell with a small spire elevated slightly and having the aperture broadly ovate. The inner lip is somewhat thickened and subangular within, giving a slight indication of a columella. In all respects it very closely resembles the typical forms of *Strophostylus cyclostomus* Hall from the Niagara shales of Waldron, Indiana. The shells described under Platystoma subsequent to the appearance of the original diagnosis vary more or less from the typical species. The general tendency, however, has been to include under Conrad's genus those forms having a rather small, depressed spire, the inner lip rather thin, and simply reflected over the body-whorl. Often the lip does not touch the second volution and the mouth of the shell is frequently free for a considerable distance. Some of these forms closely approach Paleozoic species of Capulus.

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[6] Man. de Conch., p. 756.

[7] Handb. der Palæ., I. Band, 2 Ab., p. 217.

[8] Palæ. N. Y., Vol. III., p. 303.

When, in 1859, Hall examined the interior of a Platystoma-like shell (which he afterwards called *Strophostylus andrewsi*), he found that the specimen had the inner lip considerably thickened and somewhat angular within. As a matter of course the interior angularity appeared twisted on account of the continued enlargement of the shell to the adult stage. In some individuals the thickening was considerably exaggerated, and formed a short projecting lamella or ridge. But from the figures given by Hall it is clear that this was not entirely characteristic, and the two specimens figured in the text differ widely in this particular. Nevertheless Strophostylus was proposed and has since been applied to nearly a score of species.

The limits of Conrad's and Hall's genera have never been precisely defined in the descriptions of species, and the larger majority of the forms in question have manifestly been assigned to their respective groups more on account of the general shape of the shells than from an examination of the columellar parts, which were only in exceptional cases visible without the removal of the hard matrix.

From the foregoing it is evident that Strophostylus and Platystoma are practically identical, and that therefore the two must be regarded as synonymous. The type of the first section, *Strophostylus andrewsi*, actually stands at one extremity of a rather extensive and variant series of shells of which *Platystoma ventricosum* is one of the median members. At the other extremity are the capulus-like forms, similar to those described by White and Whitfield as *Platyceras bivolve.*

The synonymy of the genus is as follows:

1842. Platyostoma, Conrad, Jour. Acad. Nat. Sci., Phila., Vol. VIII., p. 275. (Not Klein, 1753; nor Meigen, 1803; nor Agassiz, 1829.)

1859. Strophostylus Hall, Palæ. N. Y., Vol. III., p. 303.

1885. Platystoma Zittel, Hand. der Palæ., Band I., 2 Ab., p. 217.

1887. Diaphorostoma Fisher, Man. de Conchl., p. 756.

The following species are regarded as members of the Strophostylus group. Of the species originally described under this genus as understood by Hall, and under Platystoma, several have not as yet been sufficiently examined to determine definitely their generic position. The majority of those omitted, however, are mere internal casts or fragmentary individuals, which have no value whatever morphologically; and from a geologic standpoint possess only doubtfully generic interest.

Strophostylus andrewsi Hall.
Platystoma arenosum Conrad.
Platyceras bivolve White and Whitfield.
Platyceras billingsi Hall.
Strophostylus cancellatus Meek and Worthen.
Strophostylus cyclostomus Hall.
Strophostylus elegans Hall.
Strophostylus fitchi Hall.
Platystoma lineatum Conrad.
Strophostylus matheri Hall.
Platystoma niagarense Hall.
Strophostylus obtusus Hall.
Platystoma peoriense McChesney.
Platystoma pleurotoma Hall.
Platystoma strophium Hall.
Strophostylus transversus Hall.
Platystoma turbinatum Hall.
Strophostylus unicus Hall.
Pleurōtomaria unisulcata Conrad.
Strophostylus varians Hall.
Platystoma ventricosum Conrad.

Strophostylus, as now understood, embraces three rather well-marked types of shells. One of these sections contains chiefly those extreme forms upon which the genus was originally founded. These shells are subglobose, with the spire somewhat elevated; the columellar parts are prominent, and the front portion of the inner lip is considerably thickened, often having a distinct depression or groove which continues inward around the columella. This group finds its greatest development in the Upper Silurian. Another section includes shells similar to *Strophostylus* (Platystoma) *niagarensis*, in which the spire is depressed, the inner lip simply anchylosed to the body-whorl, and thickened to little or no extent. These forms predominate in the Devonian. They closely approach certain Capuli which have been called Platycerata, and it is very probable that the generic position of a number of species in the latter genus will be modified upon more critical examinations of all the forms. To the third section belong chiefly Carboniferous shells like *Strophostylus* (Platystoma) *peoriensis* McC.

The most striking points of difference in the various forms here referred to Strophostylus are found in the columellar region and along the inner margin of the aperture. The columella is in no species perforated for the umbilicus. In those species showing these parts in the greatest perfection there is a considerable thickening of the forward portion of the inner lip. This thickening is frequently more or less distinctly grooved within, parallel to the apertural margin, and consequently a prominent ridge often borders the groove towards the interior. As the shell increased in size the inner lip became reflexed, making the parts still more massive. The spiral ridge around the axis of the shell thus acquires considerable prominence in some places. In the extreme forms, as *Strophostylus andrewsi*,—the species upon which Hall based his genus,—the columellar ridge forms a kind of elevated lamella, but this exaggeration is by no means constant in the different shells of the species, and in some specimens it is scarcely more conspicuous than in certain individuals of typical *Strophostylus matheri*, or even examples of *S. cyclostomus*. Through the latter two closely allied forms the transitions are made in easy stages to *S.* (Platystoma) *ventricosus.* In some of the varietal examples of the last-mentioned species a peculiar change in the inner lip begins to make its appearance. But this feature is perhaps better shown in a large series of *S. niagarensis*, its near congener. The lip, instead of being firmly united and fused with the body-whorl, as is the case with most of the forms originally described under the genus, commences to separate from the adjoining volution. In these shells the columellar parts become greatly reduced, and even almost wholly reduced, while the thickening of the inner lip entirely disappears. Nor does the change in this feature end here. Many of the individuals show a tendency to uncoil, some of them having the last whorl separated from the preceding volution by more than half a turn (Pl. XXXIII., Fig. 3). The resemblance of certain varieties to some forms of Capulus (Platyceras of Conrad) is very striking, as has been remarked elsewhere.

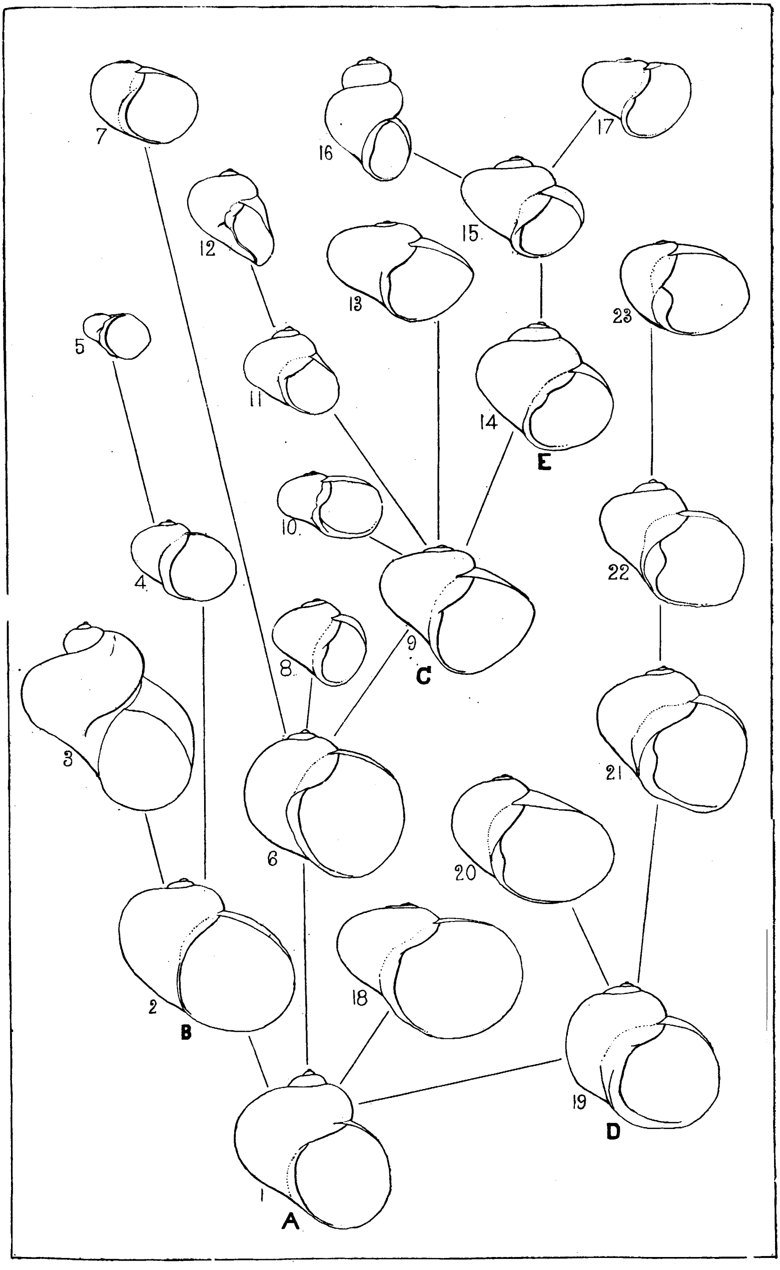
The genetic relationships, as at present understood, of the leading species of Strophostylus are graphically represented in the accompanying scheme (Pl. XXXIII.). The earliest-known forms of this group are from the Niagara rocks; but the extended vertical range of such species as *S. ventricosus* would indicate that the specific type has a higher antiquity than present information would suggest. Three principal series developed from this primitive type: (A) one preserving more or less distinctly the original characters; (B) another degenerated more or less, giving rise to loosely coiled shells and those approaching the Capulus group; and (D) a third exhibits intensified features which are particularly noticeable in the region of the columella. Fig. 1 represents the species upon which Conrad based his genus Platystoma, and was called *P. ventricosum.* It chances to be the most generalized as well as one of the oldest forms of the group. The series D showed a continued progression in the development of the axial parts, and finally ended in a form having a conspicuously twisted columella, as was acquired by *S. andrewsi* (Fig. 23). This exaggerated character in the species last alluded to was the basis of Hall's genus Strophostylus. But it will be seen at once that the species selected was actually an extreme development of a variant series, and is connected by a complete gradation of forms with the earlier and less specialized one. Later in the history of the most primitive form now known an exceedingly variable series (C) is given off, which assumes in the several species diverse characters. Some vary more towards the *S. andrewsi* type, while others tend towards the *S. niagarensis* section. In the variable forms of *S. turbinatus* some significant phases are presented which suggest the relationship of these shells to certain other genera. In the extreme form appears an elevation of the spire that is unknown elsewhere in the group. Some examples show scarcely any thickening of the inner lip or columella, while others have these features well developed.

It must be borne in mind that the scheme as here represented is intended to indicate merely the lines along which the several developments took place, rather than the phylogenetic history of the group. The correct determinations of the phylogeny of animals from paleontological evidence is attended with many difficulties. For, as repeatedly shown by Darwin and others, new variations tend to be transferred backward in the ontogenetic history of a species, and may disposess older characters. This, taken in connection with the fact that variant changes may occur in one part of an organism without materially affecting other parts, calls for extreme conservatism in passing judgment on phylogenetic problems from evidence afforded by fossils.

EXPLANATION OF PLATE XXXIII.

FIG. 1. *Strophostylus ventricosus* Conrad, Lower Helderberg. 2. *S. niagarensis* Hall, Niagara. 3. *S. niagarensis* var., Niagara. 4. *S. niagarensis* var., Niagara. 5. *S. bivolvis* White and Whitfield, Lower Carboniferous. 6. *S. ventricosus* Conrad, Oriskany. 7. *S. peoriensis* McChesney, Upper Carboniferous. 9. *S. lineatus* Conrad, Upper Helderberg. 10. *S. lineatus* var. *calosa*. 11. *S. varians* Hall, Upper Helderberg. 12. *S. varians* var., Upper Helderberg. 13. *S. lineatus* Conrad, Hamilton. 14. *S. unisulcatus* Conrad, Upper Helderberg. 15. *S. turbinatus* Hall, Upper Helderberg. 16. *S. turbinatus* var. *cochlea*, Hamilton. 17. *S. turbinatus*, var. 18. *S. expansus*, Oriskany. 19. *S. cyclostomus* Hall, Niagara. 20. *S. transversus* Hall, Oriskany. 21. *S. arenosus* Conrad, Lower Helderberg. 22. *S. matheri* Hall, Oriskany. 23. *S. andrewsi* Hall, Oriskany.

PLATE XXXIII.



STREPTOSTYLUS.